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''CONCAVE ISLANDS'': HABITAT HETEROGENEITY OF PARAFLUVIAL PONDS IN A GRAVEL-BED RIVER

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Abstract: Floodplain pond distribution, density, and diversity were investigated along the active river corridor of the Tagliamento River in northeastern Italy, the last major semi-natural river in Central Europe. Along the corridor, ponds peaked in bar- and island-braided floodplains but were absent in constrained sections. Within the main study area, a 1.0-km^2 large braided floodplain, the number of ponds containing water ranged between 18 and 39 depending on the water level in the main channel. Thermal properties and water-level fluctuations were the most important variables determining pond characteristics and heterogeneity. Results from a PCA on environmental variables distinguished four groups of ponds distributed along a hydrologic and thermal gradient. Parafluvial ponds are short-lived, discrete, aquatic ''islands'' within the floodplain matrix. They are expected to contribute disproportionately to aquatic biodiversity; however, they are very sensitive landscape elements that disappear as a consequence of river regulation, wood removal, and flow control.

Key Words: reference river, braided, restoration, biodiversity, riparian, patch dynamics

INTRODUCTION

Riparian corridors are characterized by a large diversity of aquatic and terrestrial landscape elements (Ward et al. 2002). Surface waters include lotic, semi-lotic, and lentic water bodies distributed along an inundation continuum. Cut-and-fill alluviation, coupled with ground- and surface-water interactions, create a complex array of shallow lentic habitats, including floodplain ponds. While lentic water bodies such as vernal ponds, forested wetland ponds, prairie ponds, man-constructed ponds, and small lakes have been extensively studied (Batzer et al. 1999, Schwartz and Jenkins 2000, Brönmark and Hansson 2002, Brooks and Hayahi 2002, Oertli et al. 2002), alluvial ponds have been almost completely ignored (Drago 1989, Homes et al. 1999).

Ponds are important for biodiversity conservation, but they have been lost on a large scale during the twentieth century, reaching 40–90% for Western European countries and for the U.S.A. (Hull 1997, Mitsch and Gosselink 2000, Wood et al. 2003). Ponds in dynamic floodplains are among the most endangered landscape elements since they disappear rapidly as a consequence of river regulation (Homes et al. 1999, Gurnell and Petts 2002, Ward et al. 2002). Ecologically, floodplain ponds can be viewed as ''concave islands'' that are embedded into the alluvial floodplain matrix (cf. Holland and Jain 1981).

The main objectives of the present study were to characterize the environmental conditions of alluvial ponds and to quantify their physicochemical heterogeneity. Our focus was on parafluvial (*sensu* Fisher et al. 1998) ponds within the active zone of the river corridor and the riparian forest ponds. We recognized three main questions. (1) Where do ponds peak in number along the corridor? (2) How are pond density and pond area related to river hydrology? (3) Which environmental variables explain pond diversity within the active plain? The semi-natural Tagliamento River in northeastern Italy offers the rare opportunity to study the density, diversity, and dynamics of parafluvial ponds under near-natural conditions (Tockner et al. 2003).

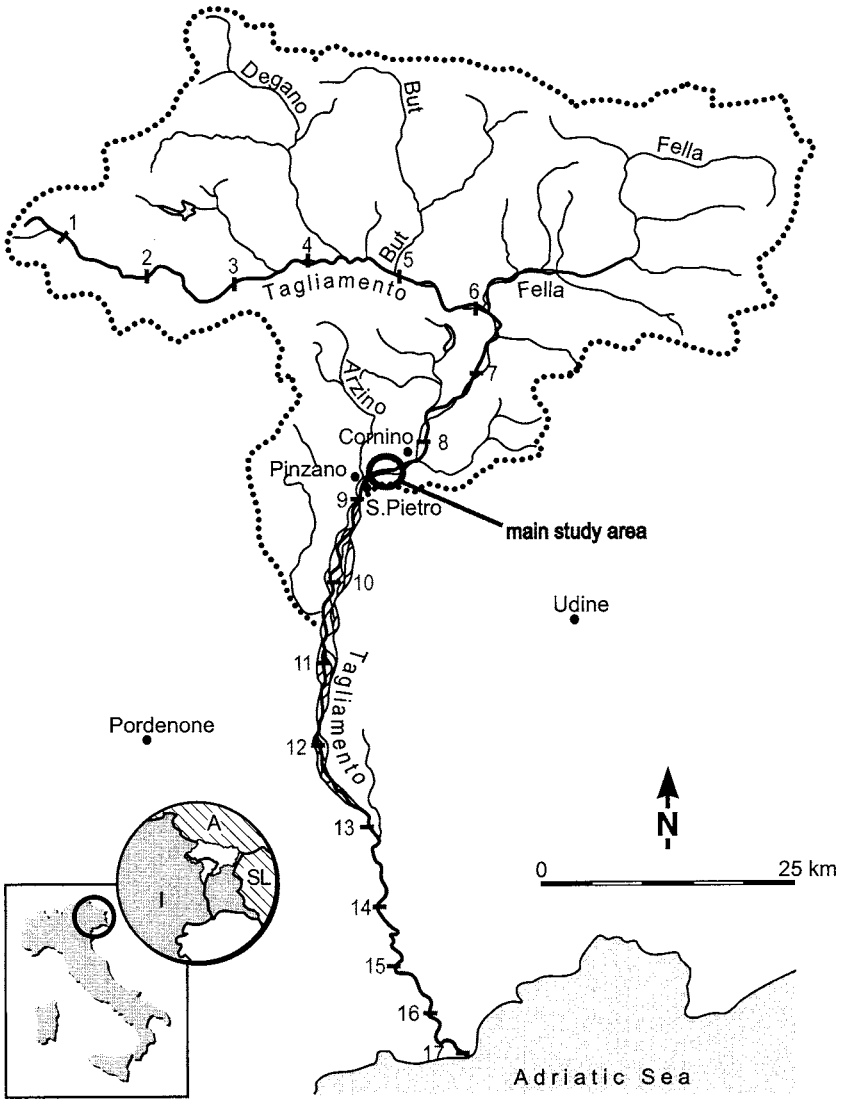

Figure 1. The catchment of the Tagliamento and the location of study sites. I = Italy, SL = Slovenia, A = Austria. Numbers (1–17) stand for the study segments of the longitudinal survey.

STUDY AREA

The Tagliamento is a large, gravel-bed river located in northeastern Italy (Friuli-Venezia Giulia; 46°N, 12°30′E; Figure 1). The river originates at 1195 m a.s.l. in the Carnian Alps and flows 170 km to the Adriatic Sea. The catchment covers 2580 km^2, with more than 70% of its catchment located in the Alps. The mountainous part of the catchment consists of limestone and Flysch deposits, and the Friulian plain is filled with Tertiary and Quaternary sediments (Petts et al. 2000, Tockner et al. 2003). The riparian corridor consists of five major landscape elements: surface water (12.4 km^2), bare gravel (38.7 km^2), vegetated islands (10.6 km^2), riparian forest (32.0 km^2), and topographical low areas that are not forested (~50-km^2, Tockner et al. 2003). The Tagliamento has an average discharge of ~70 m^{3}s^{-1}, whereas floods with 2-, 5-, and 10-yr recurrence intervals are estimated to be 1100, 1600, and 2150 m^{3}s^{-1} (Petts et al. 2000). High flow is caused by snowmelt (spring) and by heavy rainfall (autumn), with discharge maxima of ~4000 m^{3}s^{-1} (Ward et al. 1999). The near-natural morphological character of the Tagliamento is reflected by a complex channel morphology structured by a dynamic hydrologic flood regime, an idealized longitudinal sequence of constrained, braided, and meandering sections, and low human impacts. In the braided section, the active plain is up to 1.5 km wide and characterized by a variable cover of vegetated islands (Petts et al. 2000, Arscott 2001, Gurnell et al. 2001, Van der Nat et al. 2002).

The main study area is a 1-km^2 flood plain in the

middle section of the river corridor (Figure 1; river kilometer 79.8–80.8; 135 m a.s.l.). It consists of lotic and lentic water bodies (ponds), gravel bars, wooded islands, and a fringing riparian forest. The local climate has an Alpine character, with much precipitation (2000 mm yr^{-1} at Gemona at 215 m a.s.l., 1961–1990) and a mean maximum air temperature of 17.6°C. Detailed information on the catchment and the main study area are given by Ward et al. (1999), Arscott et al. (2000), Gurnell at al. (2000), and Tockner et al. (2003).

METHODS

In the present study, we defined ponds as isolated water bodies with a surface area >2 m^2 and a water depth >10 cm. Hydrologically, ponds were divided into three categories: permanent, ephemeral, and episodic. Permanent ponds carried water during the entire investigation period, ephemeral ponds dried up for some periods, and episodic ponds had surface water only during short–term flow or flood pulses (*sensu* Tockner et al. 2000).

Pond Dynamics in Space and Time

In spring 2002, around mean water level, pond density was systematically investigated within 17 segments of 1-km length; equally spaced (every 10 km) along the entire corridor (Figure 1; see also Karrenberg et al. 2003). Within each segment, all ponds were mapped.

Between April and October 2001, all ponds in the main study area were repeatedly mapped (total 46 dates). In addition to all ponds in the active zone, we included ponds in the adjacent riparian forest (right bank, in flow direction). The interval between individual sampling dates ranged from 3 to 12 days depending on the relative change of the water level (main channel). The exact position, area, and distance to vegetated islands, main channel, and side channel were measured for each pond using a Global Positioning System (GPS, TCS 1, Trimble Inc., USA). On each sampling date, shape, length, width, and maximum depth were determined for all ponds that actually contained water. The surface area of each pond was calculated during filling and drying periods by multiplying maximum length and maximum width. Furthermore, the degree of surface connectivity of individual pond with channels was recorded.

Pond Hydrology

Water level was determined by installing simple graduated staff gauges vertically at the deepest point of each floodplain pond. Staff gauges were read manually at each sampling date (totaling 46 dates). A permanent gauging station at a knick point 1.5-km downstream of our investigation site (location name: S. Pietro) was used as a reference point in the main channel. Stage data were used rather than discharge because discharge data were not available for the investigation period. A problem using stage data from a morphologically dynamic river is that channel bed elevations change frequently; these changes could affect the stage discharge relationship. The gauging station from which the data were obtained is located at a stable bedrock constriction and therefore minimized instability in the stage discharge relationship. Daily changes and cumulative water-level fluctuations (sum of daily change) were calculated for each pond.

Thermal Heterogeneity

From April to October 2001, surface-water temperature was recorded at hourly intervals. Temperature data-loggers (VEMCO Minilog, Nova Scotia, Canada) were installed at the deepest point of each pond (Arscott et al. 2001, Uehlinger et al. 2003). The following variables were calculated to characterize thermal heterogeneity: (i) average daily temperature, (ii) average minimum daily temperature, (iii) diel temperature amplitude (maximum − minimum difference), (iv) seasonal variation expressed as the difference between minimum and maximum values during the investigation period, and (v) cumulative degree days (sum of daily mean temperature).

Physicochemical Characterization

Oxygen (mg/l, % saturation) was measured with a portable oximeter (Oxi 320, WTW, Germany), pH with a portable pH meter (pH 340, WTW, Germany), turbidity (Nephelometric Turbidity Units: NTUs) with a portable turbidity meter (Cosmos, Züllig, Switzerland), and specific conductance ($\mu S\ cm^{-1}$, T_{ref} at 20°C) with a portable specific conductance meter (LF 325, WTW, Germany). All ponds were sampled between 8:00 and 11:00 a.m. at the central part of the pond to minimize diel influences (at the location of temperature loggers).

Statistical Analyses

Synchrony was used to assess the seasonal patterns in pond dynamics. Synchrony or temporal coherence is a measure of the similarity between a pair of sampling sites (e.g., Soranno et al. 1999, Kling et al. 2000, Tockner et al. 2002). High synchrony is generated when sites respond similarly to a common driver. For

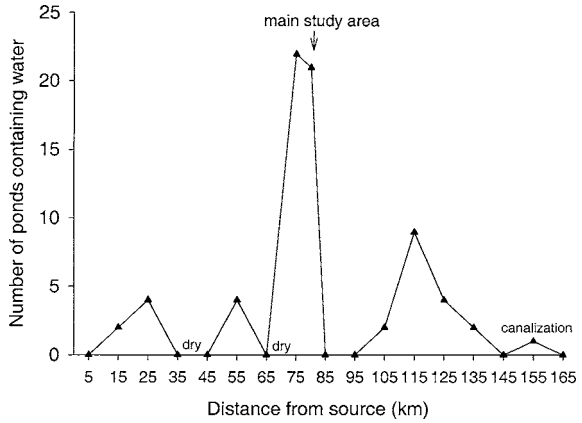

Figure 2. Number of ponds containing water per river-km along the Tagliamento corridor (April 2002).

each variable, synchrony was calculated as the Pearson product-moment correlation coefficient (r) between time series of all data (n = 46) for each pair of ponds. In order to classify individual pond types, a principal components analysis (PCA; CANOCO 4.02, Ter Braak and Smilauer 1998) was applied by integrating morphological, physicochemical, and hydrologic variables. To reflect the within- and between-pond heterogeneity, we used ranges (maximum − minimum differences) for turbidity, water-level fluctuation, specific conductance, oxygen, and pH.

RESULTS

Pond Dynamics in Space and Time

Along the active river corridor, density ranged from 0 to 22 ponds per 1-km study segment, with greatest pond density in bar- and island-braided floodplain segments (Figure 2). In 8 out of 17 segments, ponds were absent during the sampling campaign, either because there was no surface flow or because the segment was constrained naturally (canyon sections) or artificially (canalization in the most downstream sections, Figure 2).

Of the 39 ponds in the main study area, 18 were permanent, 18 ephemeral, and 3 episodic (Figure 3). Based on their location, 31% of all ponds were associated with vegetated islands, and 61% were bare-gravel ponds, the latter mostly associated with large wood accumulations. Three permanent ponds (8%) were located in the riparian forest. Pond shape was from near circular to extremely elongated, with length-to-width ratios ranging from 1.1 to 23.3.

Pond density increased exponentially from 18 ponds at a water level of 100 cm to 39 ponds at 230 cm (Figure 4). At a specific water level, the density of ponds varied considerably. For example, at a water level of 190 cm, pond density in the main study area ranged from 24 (1 May) to 32 (23 April). Based on the observed relationship between water level and pond density, an entire year of water-level data were converted into a time series of pond densities (Figure 5). As expected from this relationship, pond density strongly resembled the dynamic hydrograph, with an expected peak at ~250 cm, close to the maximum water level sampled during the present study. However, a sharp decrease in density was observed above a water level of ~250 cm (U. Karaus, personal observation). At this water level, around 50% of the floodplain is inundated (Van der Nat et al. 2002). Based on this prediction, about 50% of all ponds contained water only during short periods, often only for 1–2 days after flood events (Figure 5).

The aquatic surface area of all ponds combined increased exponentially from 1503 m^2 at low water level to 18204 m^2 at 216 cm ($y = 113.3\ e^{0.022x}$, $r^2 = 0.92$). Area of the smallest permanent pond (39) was 3 m^2 at lowest measured water level and 48 m^2 at highest water level. Pond 92 was the largest pond at lowest water level (618 m^2). At highest measured water level, pond 82 was the largest pond (7965 m^2). The area ratio of high to low water level (A_{high}/A_{low}; Table 1) ranged from 2 (pond 33) to 470 (pond 82).

Pond Hydrology

During the investigation period, the maximum change in water level ranged from 11 cm (pond 93) to 72 cm (pond 84), compared to 116 cm in the main channel (Figure 6). Cumulative water-level change (sum of daily changes during the investigation period) ranged from 56 cm (pond 93) to 311 cm (pond 94), compared to 348 cm in the main channel. A distinct hydrologic gradient occurred across the floodplain. Ponds close to the right bank (in flow direction) had small water-level fluctuations, ponds close to the main channel and ponds located in former channels (ponds 82, 79) showed large amplitudes (Figure 6). Water-level fluctuations in all permanent ponds except pond 102 were strongly related to the hydrograph of the main channel ($r > 0.5$). Pond 102 had a very constant water level.

At low water level (100 cm), 54% of the ponds were dry and 46% remained disconnected. At mean water level (189 cm), 31% were dry, 64% remained disconnected, and 5% were already connected. At about 340 cm, all water bodies (ponds and channels) merged into a single channel (Figure 7).

Thermal Heterogeneity

Over the 6-month period (May to October 2001), cumulative degree-days were from 1924°C (pond 102)

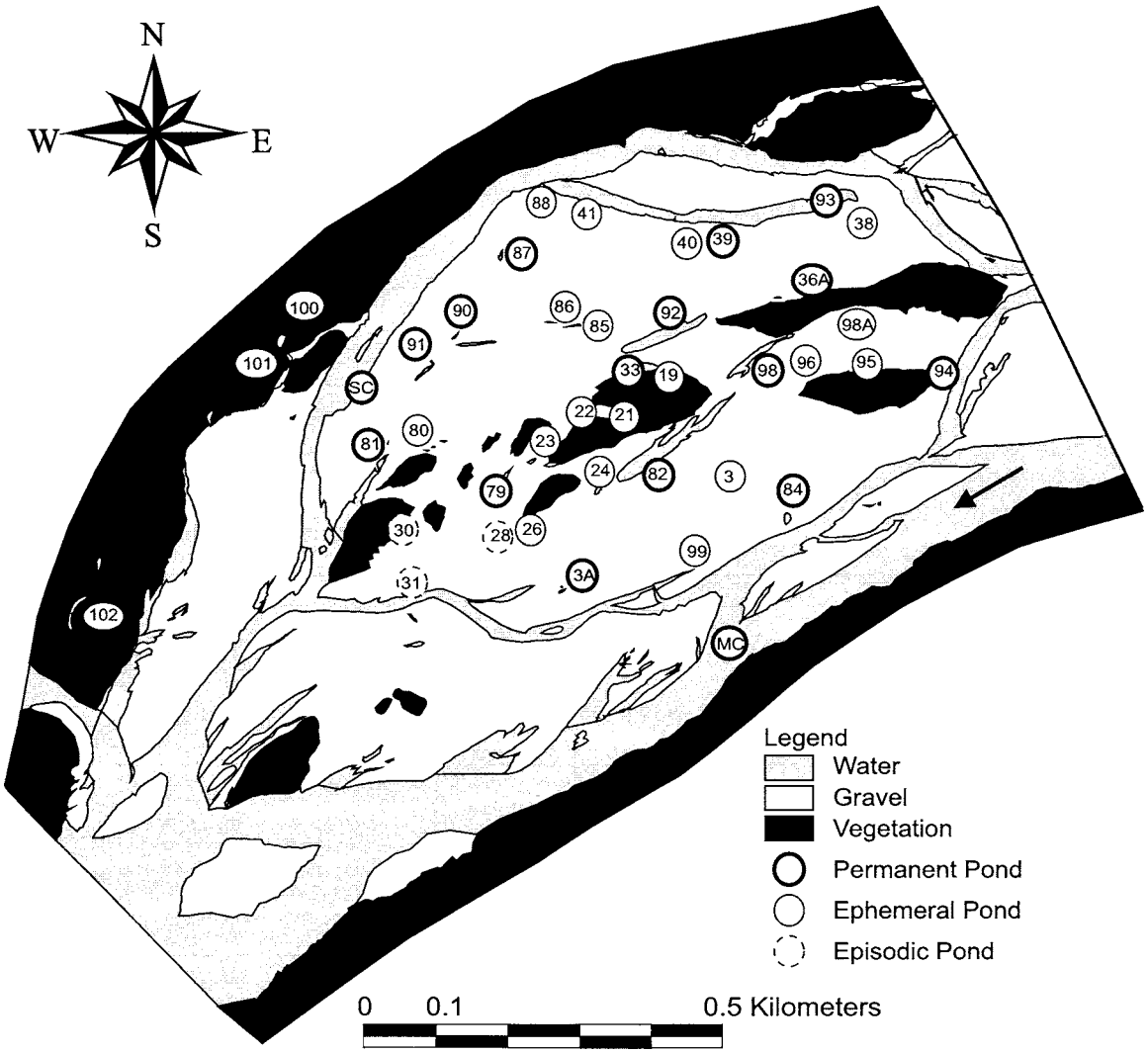

Figure 3. Map of the main study area and location of permanent, ephemeral, and episodic ponds. In the active corridor, only ponds within the large gravel bar / island complex were considered. Ponds 100 to 102 are in the riparian forest.

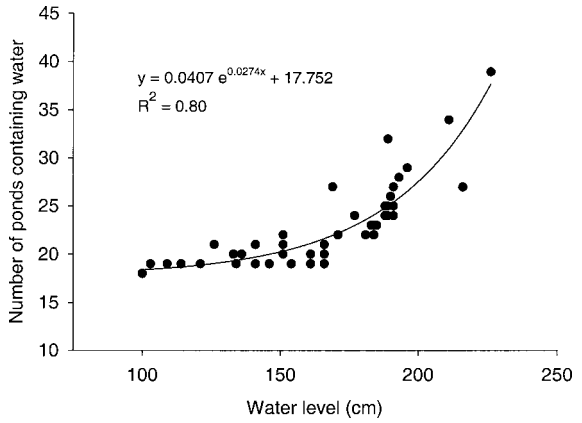

Figure 4. Relationship between water level of the main channel (S. Pietro) and the number of ponds containing water.

to 3308°C (pond 87). Across the floodplain, average daily temperature difference between the coolest and the warmest pond ranged from 4.0°C to 16.1°C, with an average difference of 9.8°C. Within individual ponds, average daily temperature (May until October) ranged from 13.4°C (pond 102) to 22°C (pond 92), and average diel amplitude was from 0.9°C (pond 102) to 11.6°C (pond 92). Maximum diel amplitude was between 1.3°C (pond 102) and 26.2°C (pond 39). Individual ponds can be arranged across a gradient from small to large diel and seasonal amplitudes (Figure 8). Diel and seasonal temperature patterns (based on hourly measurements) illustrate differences in thermal regimes across the floodplain (Figure 9). Pond 33, for example, had low diel variation but a distinct seasonal variation. A similar seasonal variation, but with larger daily fluctuations, was observed in pond 36A. Distinct diel temperature fluctuations were measured in ponds

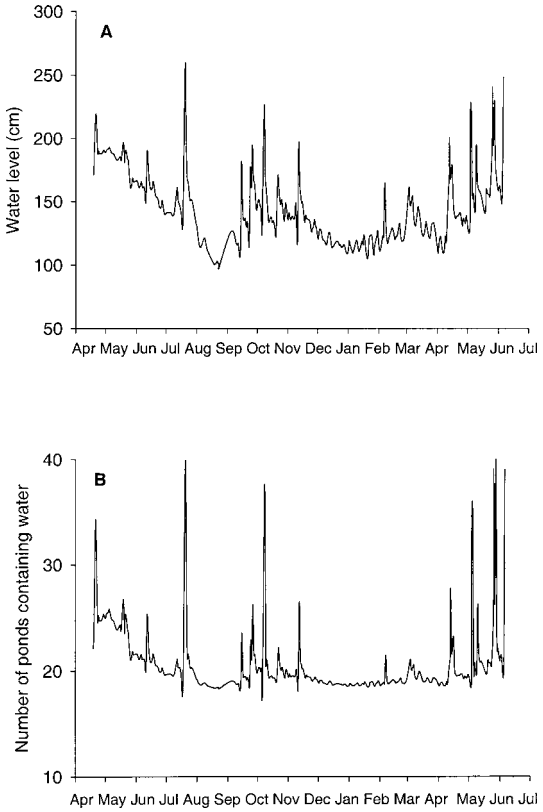

Figure 5. A: Water level (S. Pietro) from May 2001 to June 2002. B: Number of ponds predicted from the water level—pond number relationship (see Figure 4) for this time period.

Table 1. Area (m^2) of selected floodplain ponds at low water level (A_{low}; 103 cm) and high water level (A_{high}; 216 cm), and area variation (ratio A_{high}/A_{low}).

Pond	A_{low}	A_{high}	A_{high}/A_{low}
3A	36	239	7
33	173	408	2
36A	6	85	15
39	3	48	16
79	289	2718	9
80	5	86	18
81	63	165	3
82	17	7965	469
84	70	321	5
87	39	150	4
92	618	4343	7
94	17	268	16
98	167	1345	8
98A	0 (dry)	64	>64

88, 90, 92, and 94. Small temperature fluctuations at the beginning of the investigation period and a continuous increase during the investigation period were featured in pond 90. A weak seasonal temperature pattern was shown in ponds 98 and 102.

Classification of Ponds

Average synchrony for all variables was 0.33. This average was taken across all pairs of ponds. Synchrony of individual ponds with all other ponds was low and ranged from 0.21 (pond 100) to 0.47 (pond 84). Synchrony between individual ponds and the lotic channel

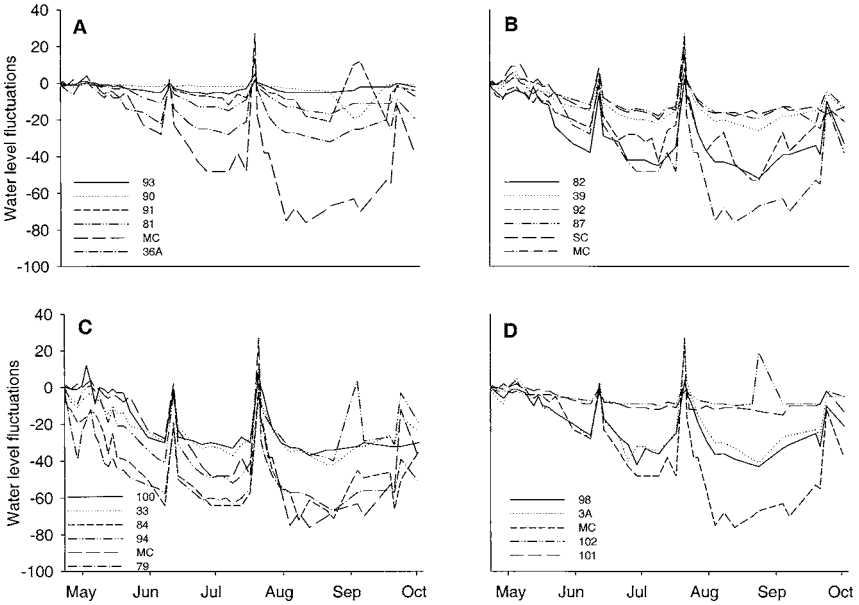

Figure 6. Relative daily water-level changes (cm) of all permanent ponds compared to the main channel (MC) during the investigation period. Ponds are grouped according to the outcome of the PCA (see Figure 10).

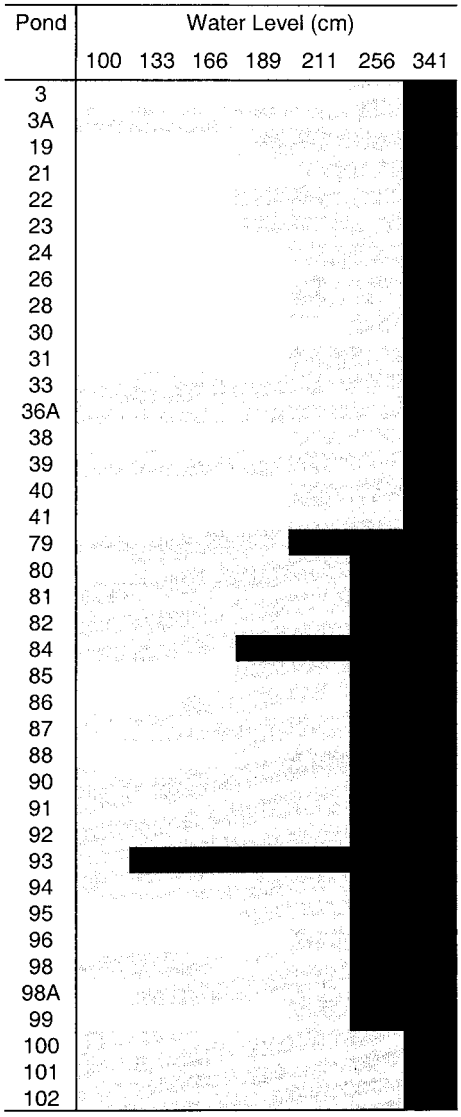

Figure 7. The shift of ponds from a dry (white) to a disconnected lentic (gray) and finally to a connected (black) state with increasing water level in the main channel (S. Pietro). Data from the water level 256 cm are obtained from a preliminary sampling in March 2001.

ranged from 0.15 (pond 15) to 0.53 (pond 53). Synchrony of variables was 0.18 for turbidity, 0.22 for specific conductance, 0.42 for pH, and 0.50 for dissolved oxygen.

The first two axes of the principal components analysis PCA explained 51% of the total variance within the data matrix (14 environmental variables, 18 permanent ponds). Average, maximum, and minimum daily temperature (73%, 64%, and 56%), water-level fluctuation (67%), turbidity (42%), and specific conductance (28%) accounted for the definition of the F1 axis (Figure 10). Average water depth (45%), average diel temperature amplitude (45%), and pH (31%) accounted for most of the definition of the F2 axis. Distance to channel and island (69 and 46%) and variability in surface area (40%) accounted for the definition of the F3 axis (not shown in Figure 10). Oxygen (77%) explained the F4 axis (not shown). Results from the PCA on these environmental variables distinguished four groups of ponds along the F1 and F2 axis (Figure 10). Group 1 (39, 82, 87, and 92; see Figure 3 for location) was characterized by a large thermal heterogeneity. In contrast, group 2 (3A, 93, 98, 101, 102) had a very low thermal heterogeneity. Group 3 (33, 79, 84, 94, 100) was hydrologically very dynamic and had a wide range in specific conductance, turbidity, pH, and oxygen values. Group 4 (81, 90, 91, 93) had small water-level fluctuations and showed a narrow range in specific conductance, turbidity, pH, and oxygen values. Pond 36A did not fit into any of the groups.

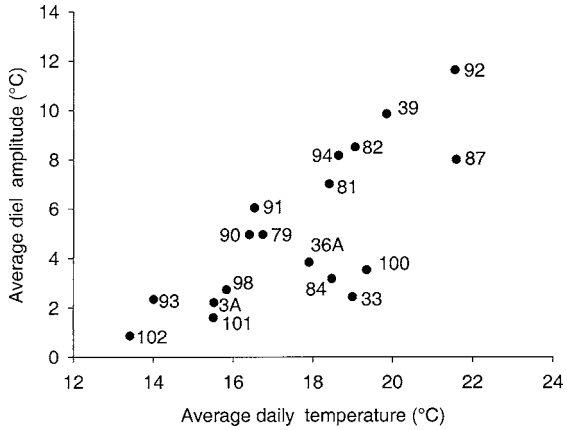

Figure 8. Average daily temperature (May until October 2001) vs. diel amplitude for all permanent ponds ($r^2 = 0.58$).

DISCUSSION

The Tagliamento River offers the rare opportunity to investigate ecosystem patterns and processes under semi-natural conditions that can be studied almost nowhere else in Europe (Ward et al. 1999). The Tagliamento has a number of attributes that have not been given due consideration in river ecology: (i) an immense corridor of more than 150 km^2, (ii) unconstrained floodplain segments, and (iii) a large number of vegetated islands (Tockner et al. 2003). A high diversity of parafluvial ponds is considered as an additional key attribute along the dynamic river corridor that has not yet been studied in detail.

Pond Dynamics in Space and Time

Along the active corridor of the Tagliamento, a maximum of 22 ponds per river-km was quantified

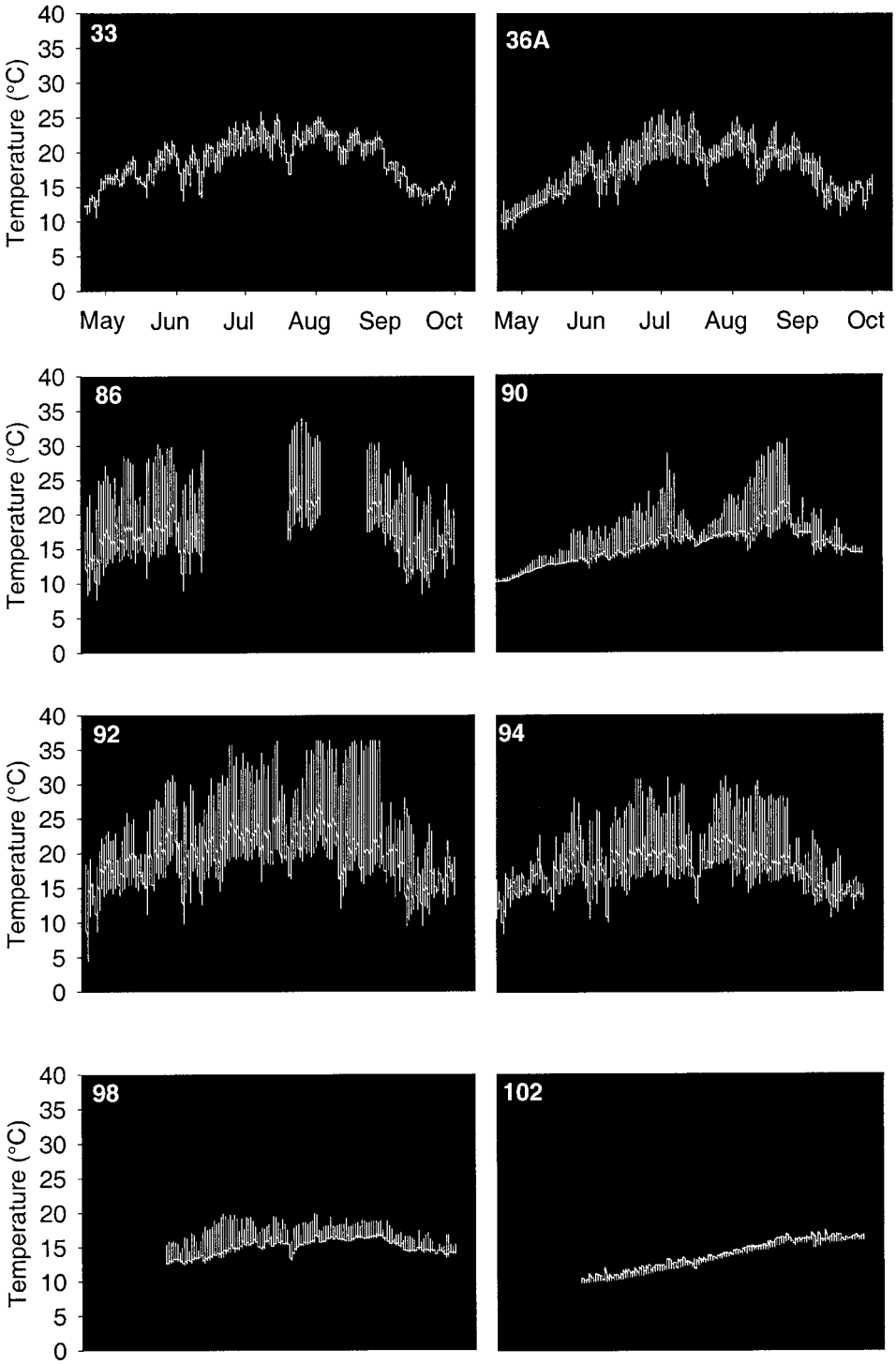

Figure 9. Hourly values of surface temperature in eight selected ponds (April to October 2001).

(Figure 2). Ponds were absent in human-controlled sections. Therefore, ponds can be considered as very sensitive aquatic habitats that disappear rapidly as a consequence of human impacts such as canalization or flow control. Along the Isar River (Germany), intensive hydrologic engineering has also led to a major decrease in pond density and heterogeneity (Homes et al. 1999).

Besides human impacts, changes in the hydrologic and geo-morphological style along the river corridor control pond density and diversity. In the headwater section, a narrow floodplain, a steep channel slope

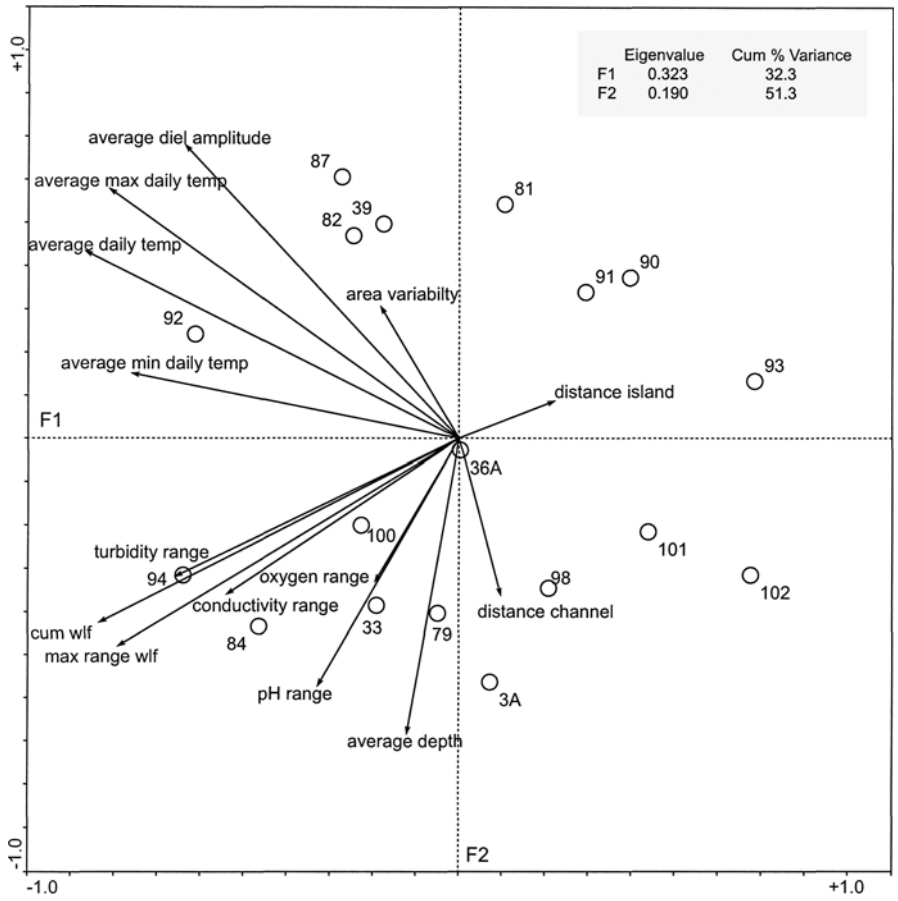

Figure 10. Principal components analysis ordination based on fourteen environmental variables for the ponds. Circles with numbers represent ponds and arrows indicate different variables. The ordination map illustrates the relationship of each variable with the definition of either the F1 or F2 axis and of each sampling point (pond) with respect to the F1 and F2 axes (defined by the variables). Average max daily temp = average maximum daily temperature; average min daily temp = average minimum daily temperature; average daily temp = average daily temperature; cum wlf = cumulative water-level fluctuation; max range wlf = maximum range of water-level fluctuation.

with coarse sediments, and a low alluvial reservoir limit the formation of ponds. An increase in active floodplain width, higher flow rates favor the formation of floodplain ponds in the middle or braided sections. In the meandering section, an increase of the active channel width combined with a narrow active floodplain corridor, and a higher alluvium results in the formation of fewer but larger ponds (Arscott et al. 2000).

Parafluvial ponds differ from woodland ponds, marshy ponds, or prairie ponds. They are very young habitats that are formed and shaped by repeated cut-and-fill processes (Kohler et al. 1999, Arscott et al. 2002). Indeed, ponds are among the youngest habitats in the Tagliamento channel, with average half-life expectancies of less than seven months (Van der Nat et al. 2003). Gravel deposition, as well as erosion, is responsible for the low half-life expectancies of ponds. Hydrologically, parafluvial ponds are closely linked to the main channel. Therefore, water-level fluctuations in the main channel control the number and areal extent of ponds (Figure 5). In the Tagliamento floodplain, an exponential relationship between water level and pond density has been observed (Figure 4). Therefore, even moderate flow fluctuations can have major consequences for both pond density and area.

Pond Hydrology and Thermal Heterogeneity

The two most important factors that control pond diversity are hydrology (source and pathway of water) and temperature (see Figure 10). Hydrologic and thermal differences among ponds can be explained by a combination of flow paths (alluvial and hill-slope ground water), pond location (shading, distance to the channel), and topography (ratio of low-to-high water surface area). For example, a decreasing trend in flow variability from the main channel towards the riparian forest was observed. The ‘‘forest ponds’’ (e.g., 102),

which were almost completely shaded, deep, and fed by hill-slope ground water, had almost no water-level fluctuations.

The variability of water level affects area, which again influences surface connectivity (lateral connectivity) between ponds and the channel. Water-level fluctuation, topography, and spatial location of each pond create a heterogeneous pattern of connectivity (Figure 7). During low water level, most ponds are disconnected and expected to function ecologically as (concave) islands. Flood events connect the islands with the river and support the exchange of matter and organisms between lotic and lentic habitats (Drago 1989), a primary factor for ecosystem dynamics and functioning. Connectivity influences, for example, diversity and productivity across different hierarchical scales (Amoros and Roux 1988, Ward and Stanford 1995, Stanford et al. 1996, Tockner et al. 1999, Ward et al. 1999). Hydrologic connectivity, which includes longitudinal, lateral, vertical, and temporal connectivity, as well as complex habitat gradients, are strongly related to high species and life-history-strategy diversity (Amoros and Bornette 2002).

The second most important factor controlling pond diversity is temperature. The investigated ponds provided a diverse array of warm and cold water patches within the active floodplain. In addition to longitudinal patterns in water temperature, lateral (e.g., ponds, backwaters) and vertical (e.g., within the substrate) heterogeneity in temperature is increasingly recognized as a potentially important aspect in habitat conditions in streams and rivers (Poole and Berman 2001, Arscott et al. 2002, Claret et al. 2002). In the main study area, a lateral thermal difference of up to 17°C at a specific day is as high as along the entire 170-km long river corridor (Arscott et al. 2001). Temperature is a primary factor that regulates ecosystem processes and therefore structures biotic communities (Ward and Stanford 1982, Ward 1992). It has a strong influence on life history, species diversity, and abundance levels (Ward and Stanford 1982).

Pond Heterogeneity and Ecological Role

Floodplain ponds had a wide range in size, shape, and physicochemical properties. An average synchrony among ponds of 0.33 indicates a low temporal coherence of ponds to a common driver (water source, flow path, temperature). Furthermore, the low average synchrony value between ponds and the lotic channel (0.31) indicates that physicochemical parameters are strongly influenced by local factors such as the topographic position of ponds, morphology, and their subsurface connectivity (i.e., ground-water exchanges). An example of local influences was demonstrated using the relationships with specific conductance, which can be used as an indicator of hydrologic connectivity. In instances where specific conductance correlated poorly between ponds and side channel, while water-level fluctuation between ponds and the main channel were highly correlated, the interpretation suggests hydrostatic effects, which indicate a hydrostatic water connection but no water exchange between ponds and channels.

The morphological, topographical, hydrologic, thermal, and physicochemical heterogeneity, which is strongly related to the local environment of each pond leads to a unique pond mosaic (Figure 10). Floodplain ponds are responsible for much of the variation in chemical conditions and thermal variability across the floodplain (Arscott et al. 2000). In contrast, they only cover a tiny portion of total aquatic surface area. In the main study area of the Tagliamento, for example, ponds contribute ~6.0% of the total aquatic surface area at low water level and <1.0% at high water level (Van der Nat 2002). Despite this small aerial extent, ponds are expected to play a crucial ecological role. Floodplain ponds can provide habitat for a specific fauna and flora as demonstrated in recent investigations along the Isar (Germany, Homes et al. 1999), in the Luznize floodplain (Czech Republic, Pechar et al. 1996), along the Ain and Rhône Rivers (France, Castella et al. 1991), or along the Flathead River (Montana, J.A. Stanford and M. Lorang, pers. comm.). The faunal community composition depends on pond age (Schneider and Frost 1996), the frequency of flooding and drying (Castella 1987), on area and spatial arrangement within the landscape (Brönmark 1985, Ward and Blaustein 1994, Oertli 2002), on depth and width (Amoros 2001), and on the frequency, duration, magnitude, and timing of flooding and drying (Brooks 2000). This supports our assumption that each pond has an insular nature (''concave island'') with a characteristic set of environmental properties. Lastly, many ponds are associated with vegetated islands. Indeed, the presence of vegetated islands enhances the diversity of aquatic habitats (Arscott et al. 2000, Gurnell et al. 2001, Gurnell and Petts 2002). Therefore, ponds are expected to contribute to a greater invertebrate diversity within the active floodplain channel.

CONCLUSIONS

The present study characterized and quantified the spatiotemporal dynamic that characterizes parafluvial ponds. Basically, all ponds are strongly related to the hydrologic regime of the channel. However, the morphology, topography, and the physicochemical properties of each pond form a heterogeneous pattern in space and time. Thereby, each pond contributes to the

overall habitat diversity of the floodplain. The longitudinal investigation not only showed ponds as part of the corridor, but also emphasized the sensitivity of ponds to anthropogenic impacts. Therefore, parafluvial ponds can be used as sensitive indicators, similar to vegetated islands (see Tockner et al. 2003), of the integrity of entire river corridors.

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